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Adaptive dynamics

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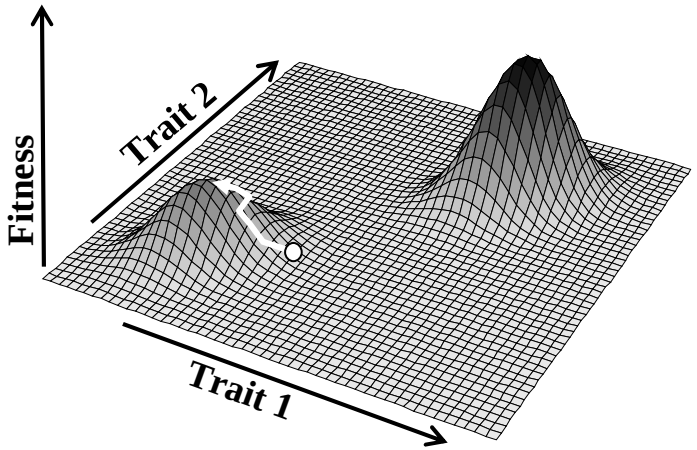
cirad
AGRICULTURAL RESEARCH
FOR DEVELOPMENT

Frequency-dependent selection

- Fundamental theoretical approaches more or less explicitly deal with optimizing selection
  - Fisher (1930), “fundamental theorem of natural selection”, mean population fitness increases monotonically over the course of adaptive evolution (provided constancy of fitness values)
  - Wright (1932), adaptive evolution as a hill-climbing process on a fixed fitness landscape

– Levins (1962a, 1962b, 1968), fitness-set approach is based on the assumption that, within a set of feasible phenotypes defined by a trade-off, evolution maximizes fitness

– Stearns (1992) Roff (1992), life-history theory - adaptive evolution optimizes a suitably chosen measure of fitness, such as the basic reproduction ratio R0

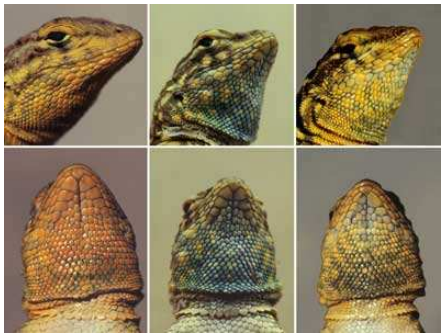


Frequency-dependent selection

- Frequency-dependent selection applies when selection pressures depend on the phenotypic composition of a population

- Frequency-dependent selection is (and in principle should be) common in nature

  e.g., colour polymorphisms, self-incompatibility alleles, sex-ratio, MHC, flu evolution, niche specialization



Side-blotched lizards (*Uta stansburiana*) play a rock-paper-scissors game

- Adaptive dynamics "is" a "conceptually unified, ecologically realistic, and technically versatile" modelling framework to account for frequency-dependent selection (Dieckmann, IIASA Website).

Modelling frequency-dependent selection

- Roots in evolutionary games theory (Eshel and Motro 1981; Eshel 1983; Taylor 1989; Hofbauer and Sigmund 1990), population genetics (Christiansen 1991; Abrams et al. 1993) and theoretical ecology (Metz et al 1992; Dieckmann et al. 1995; Dieckmann and Law 1996)

- Explicitly trades genetic realism against ecological complexity

- How does the ecological context (and its impact on population dynamics) affect selection pressures?

- “Tackling these various challenges, adaptive dynamics theory provides methods for identifying optimization principles when these exist, for predicting the course and outcome of evolution also in the absence of optimization principles, as well as for assessing the impact of evolutionary change on population viability” (Dieckmann IIASA Website).

How it works – “the mutation-limited toolbox”

Chaque individu se caractérise par sa stratégie

Trait 1

Trait 2

...

1 stratégie
=
1 ensemble de traits

Au sein d’une grande population monomorphe, dite résidente, un mutant de phénotype proche apparaît.

En supposant que chaque individu donne naissance à des individus de même stratégie que lui-même, et en se basant sur le cycle de vie de l’espèce étudiée, on peut calculer la dynamique de la population mutante au sein de la population résidente

La capacité d’un mutant à envahir le résident définit sa fitness.

3 cas sont alors possibles :

- le type d’origine gagne
- le type mutant envahit
- les deux types coexistent

En répétant cette démarche, on peut alors calculer quel(s) type(s) sera (seront) présent(s) à long terme.

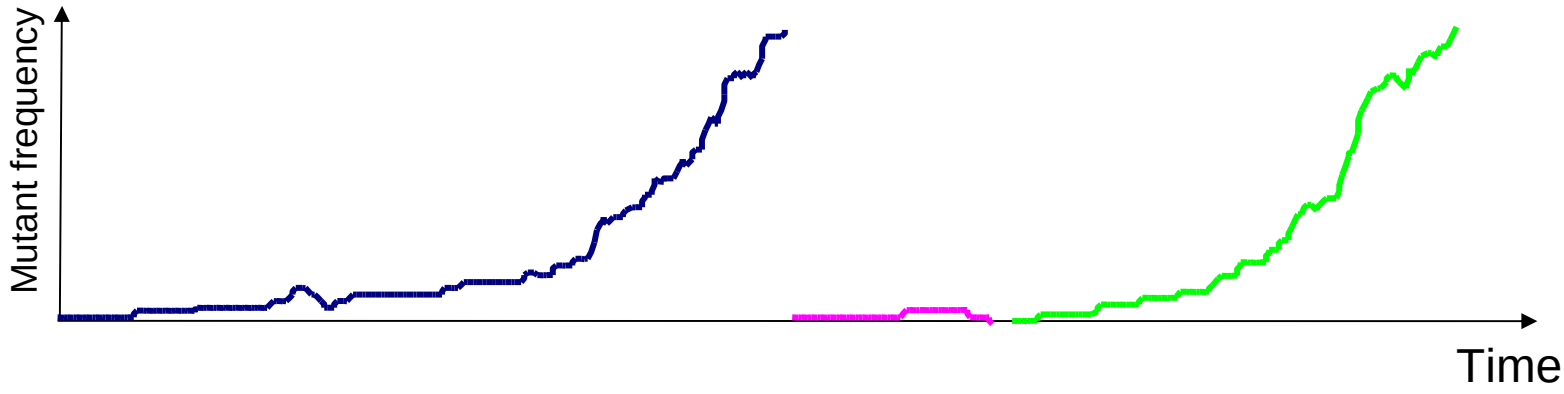
How it works – “the mutation-limited toolbox”

A finite number of well-known assumptions:

- Reproduction clonale : un individu donne naissance à des individus de même stratégie

- Résident à l’équilibre démographique
- L’effectif du mutant est initialement négligeable devant celui du résident

- Mutations de faible effet : mutant et résident se ressemblent
- Mutations rares...un mutant à la fois !

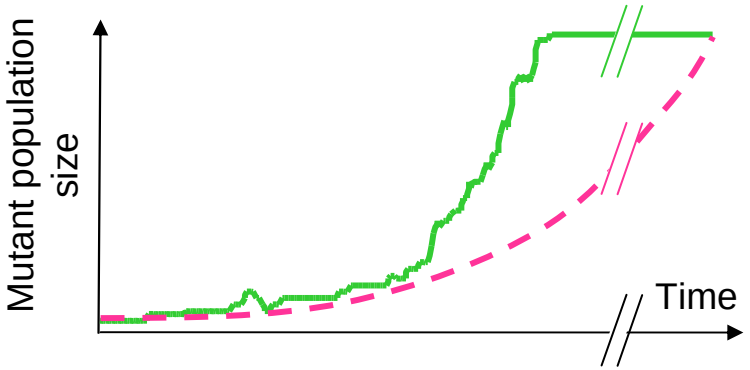


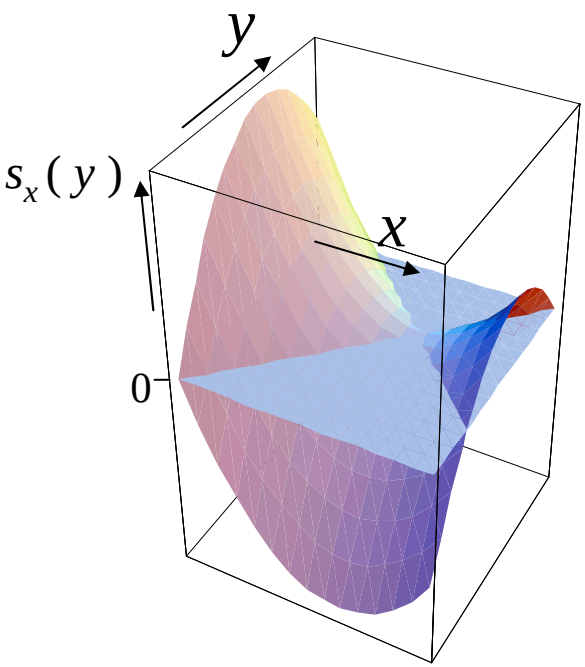
How it works – “the mutation-limited toolbox”

La fonction d’invasion, une mesure de fitness

En temps discret:

$$s_x(y) = \lim_{t \to +\infty} \left[\frac{1}{t} \ln \left(\frac{N_y(t)}{N_y(0)} \right) \right]$$





Elle permet de savoir quels mutants peuvent envahir quels résidents :

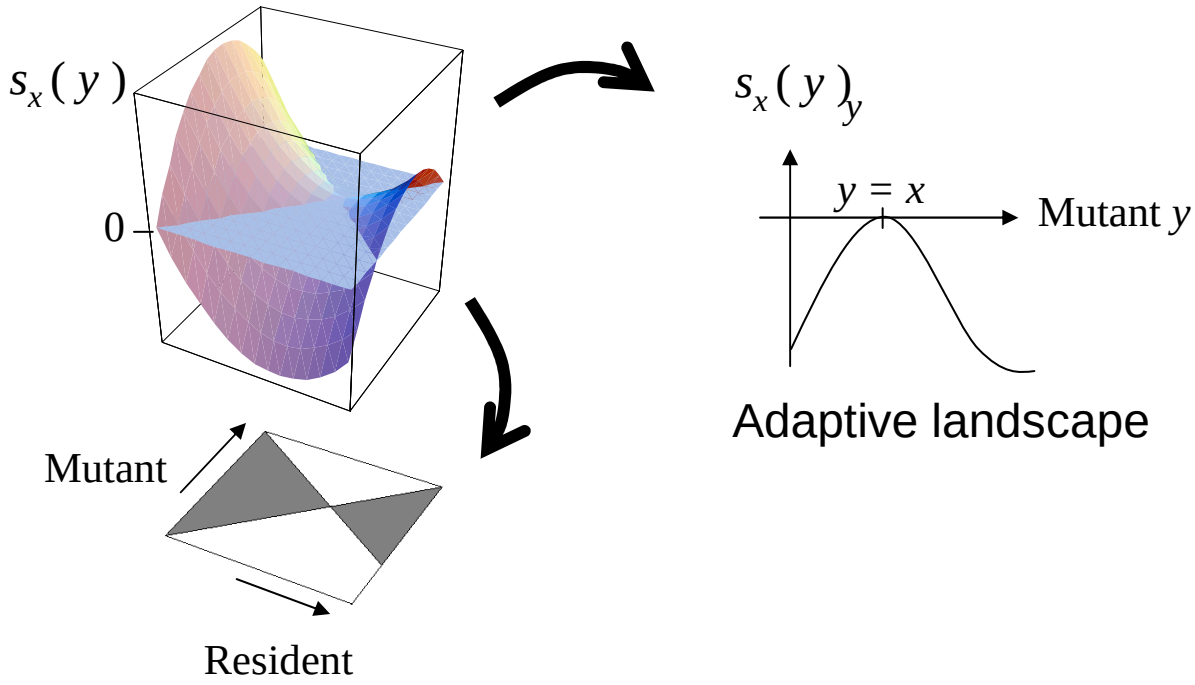
- si $s_x(y) < 0$ le mutant est éliminé
- si $s_x(y) > 0$ le mutant augmente en fréquence et envahit

Elle intègre la complexité écologique sous forme d’une dynamique de population (d’invasion)

How it works – “the mutation-limited toolbox”

Studying the shape of the invasion function allows
to determine the outcome of evolution

Mathematical + graphical tools

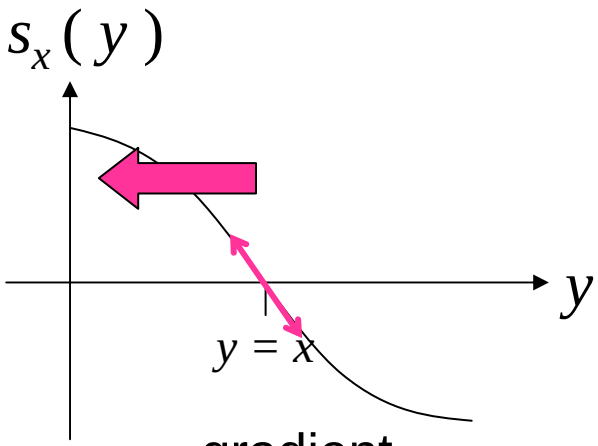


Adaptive landscape

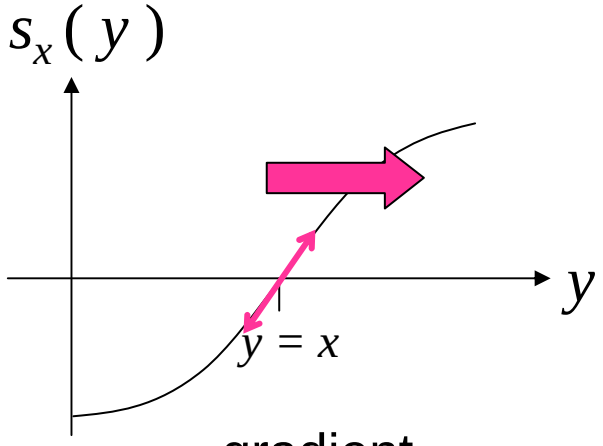
Pairwise invasibility plot

Singular strategies

Le gradient de sélection donne la direction de la sélection

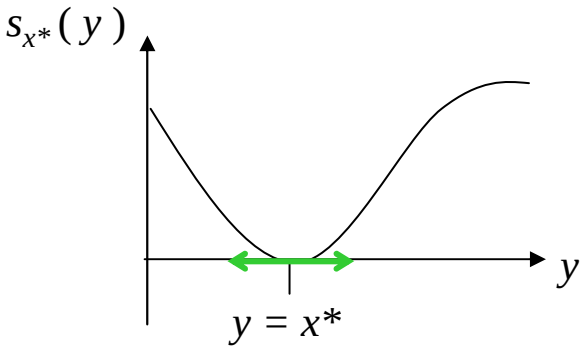


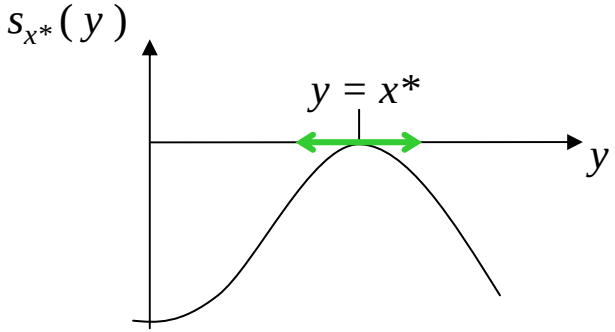
gradient négatif



gradient positif

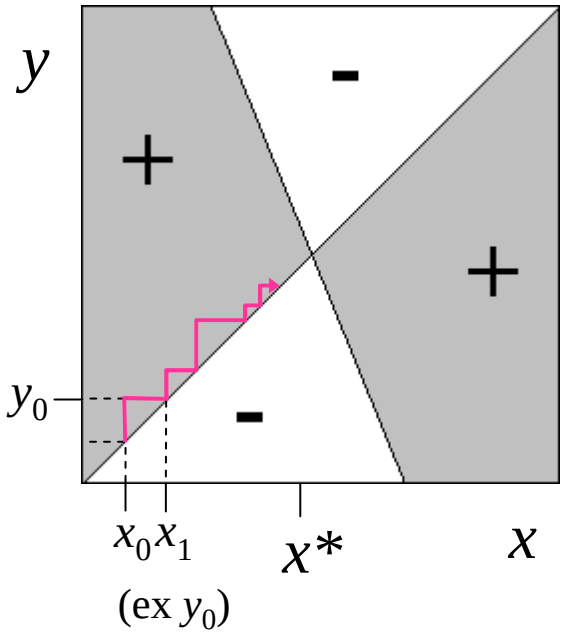
Singular strategies are those where the selection gradient vanishes



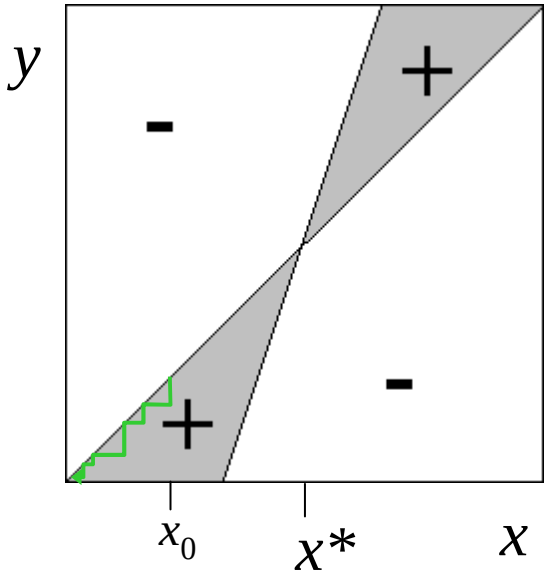


Convergence stability

Une stratégie ne peut être atteinte par petites mutations
que si elle est stable par convergence



x^* est stable par convergence

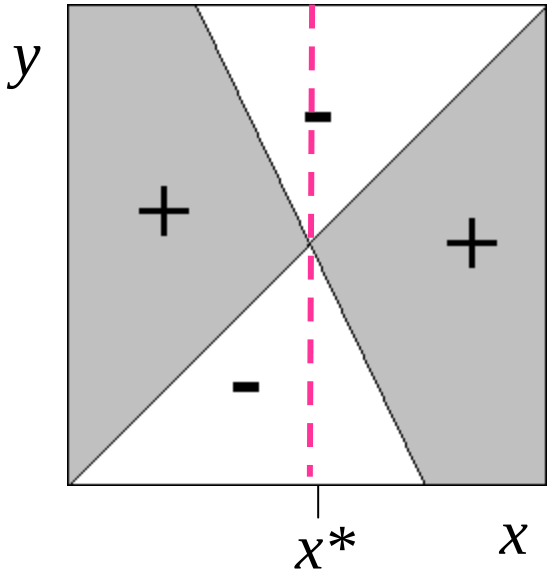


x^* n'est pas stable par convergence

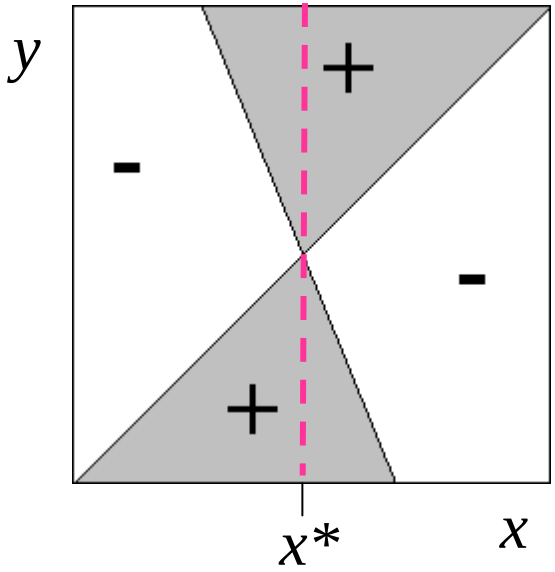
Une stratégie stable par convergence est un attracteur évolutif

Evolutionary stability

Une stratégie singulière est stable par évolution
si aucune autre stratégie ne peut l'envahir.

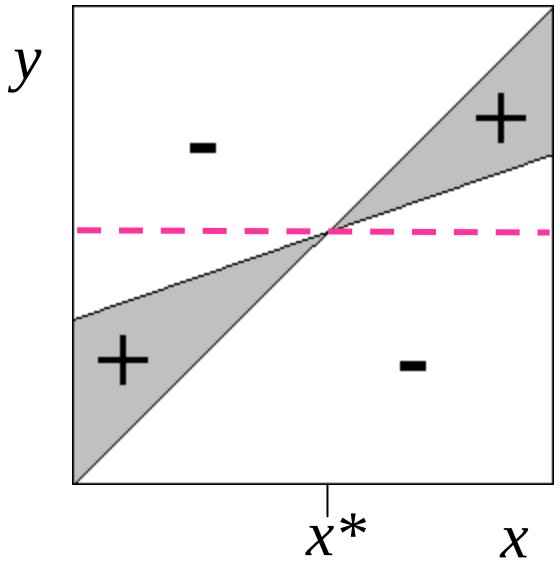


*x** est stable par évolution

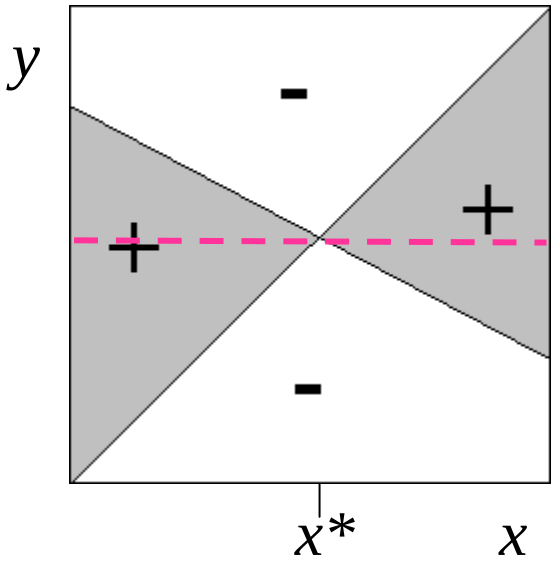


*x** n'est pas stable par évolution

La capacité d'invasion



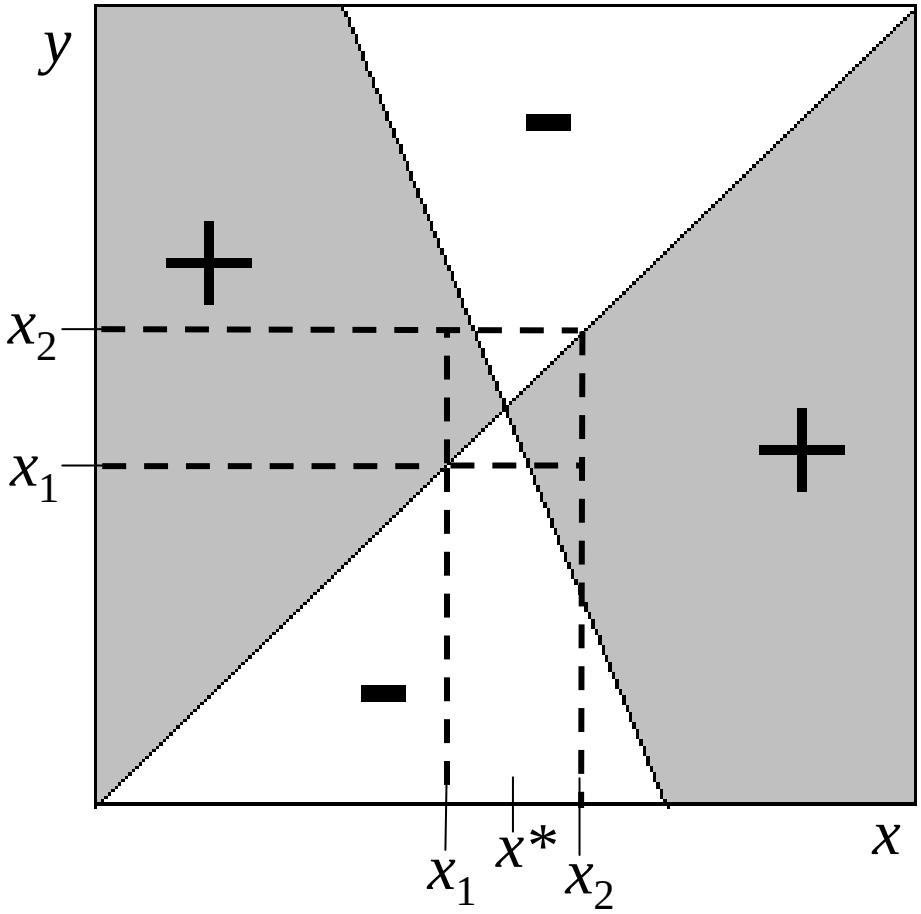
x^* ne peut jamais envahir quand elle est initialement rare



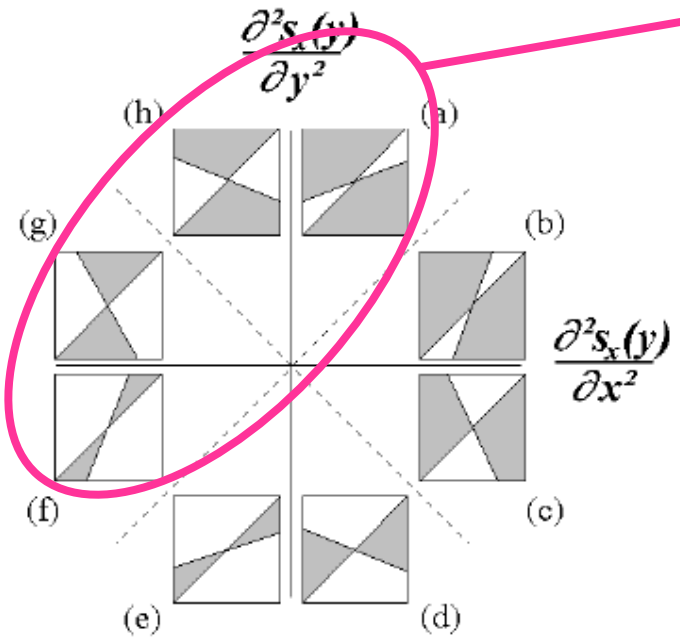
x^* peut envahir quand elle est initialement rare

Mutual invasibility

Deux stratégies et peuvent s'envahir mutuellement et éventuellement donner naissance à du polymorphisme si $s_x(y) > 0$ et $s_y(x) > 0$



A simple classification of singular strategies



Repellors

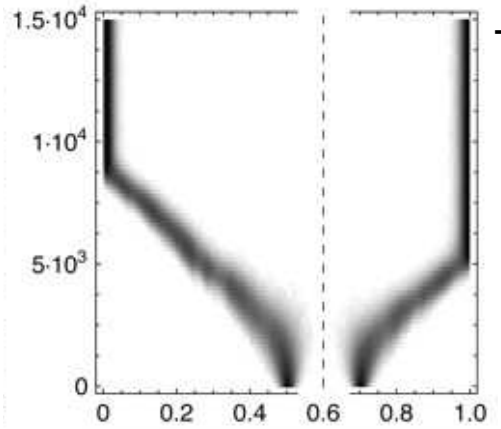
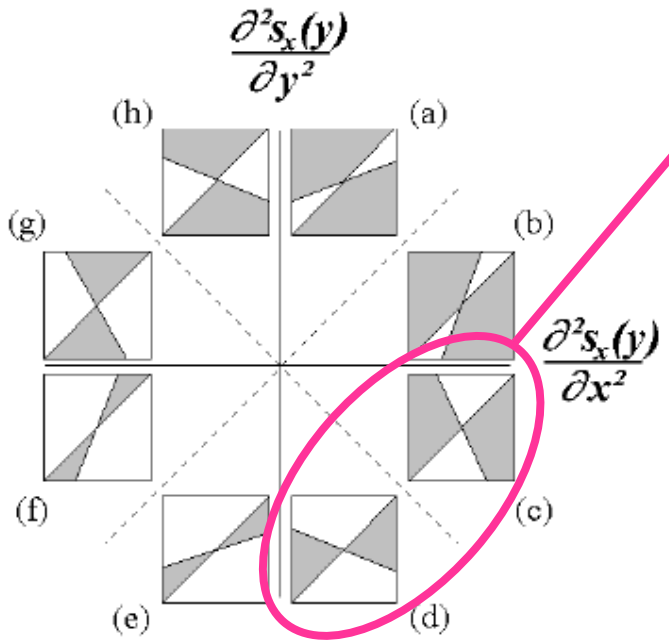


Figure 2. The eight possible generic local configurations of the pairwise invasibility plot and their relation to the second-order derivatives of $s_x(y)$. Inside the shaded regions within each separate plot, $s_x(y)$ is positive.

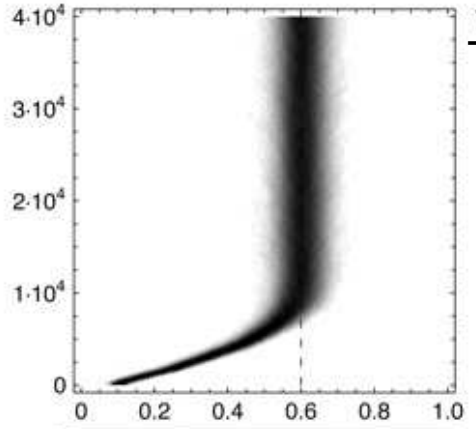
Geritz et al. 1998

Figures from Doebeli et al. 2004 Science

A simple classification of singular strategies



Evolutionary end-points



Time

Trait value

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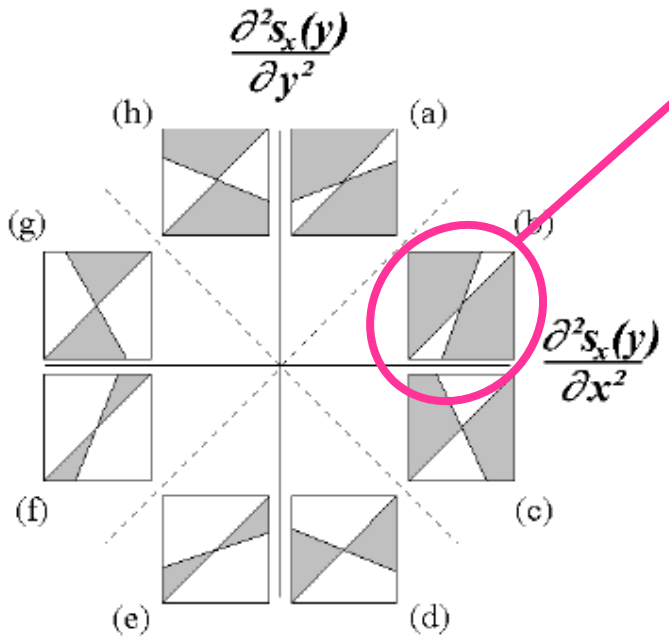
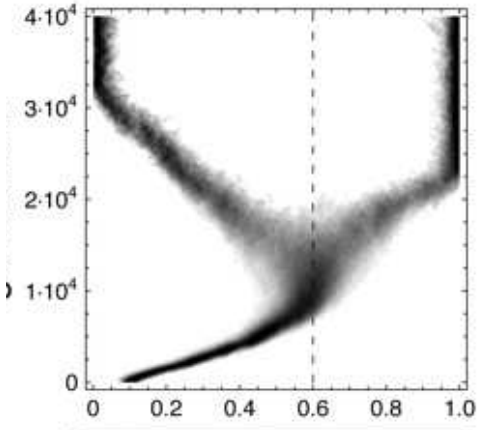


Branching points



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Geritz et al. 1998

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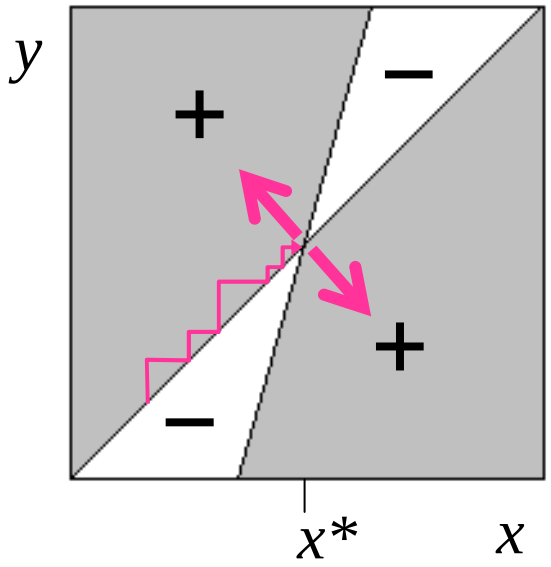
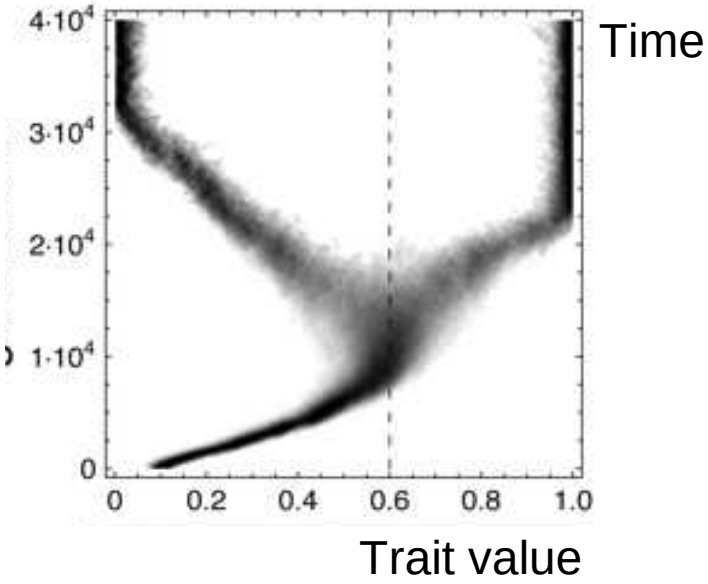
Branching points

Du polymorphisme durable peut apparaître au voisinage d'une stratégie singulière si elle est:

- Stable par convergence
- Telle que deux stratégies situées de part et d 'autre de la stratégie singulière peuvent s'envahir mutuellement
- Non stable par évolution



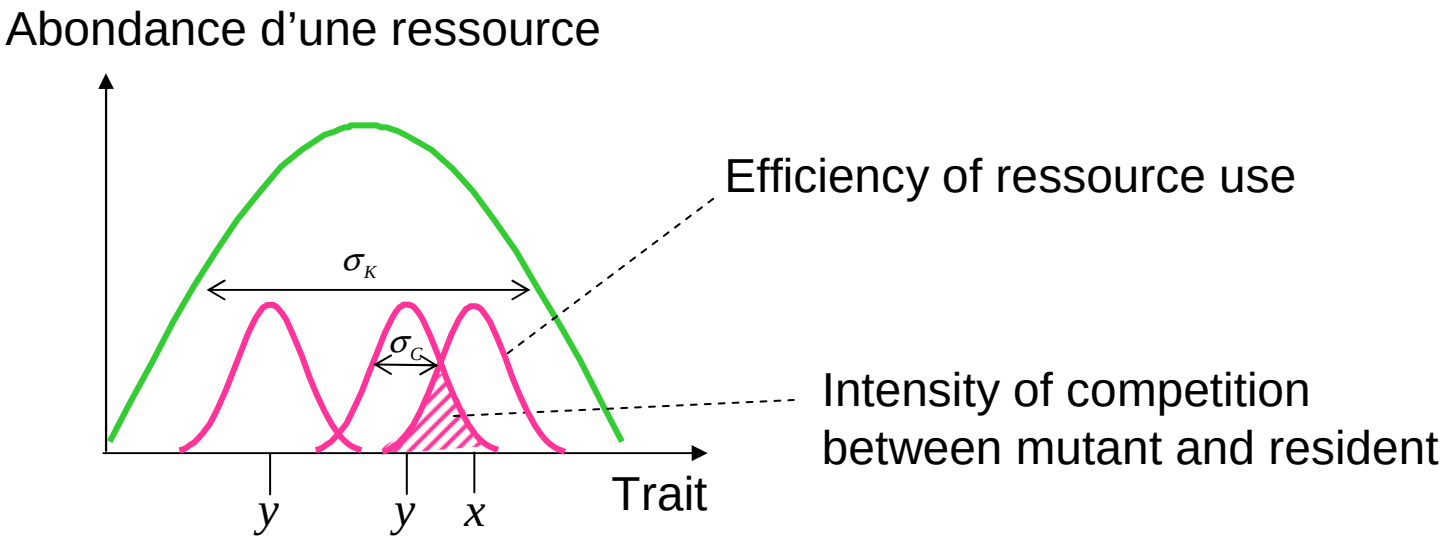


Favorite topics of adaptive dynamics

- Adaptive Dynamics Theory
- Evolution of dispersal
- Optimal foraging theory
- Evolution of niche specialization
- Evolution of host-parasite interactions and virulence Management
- Evolutionary Fisheries Management
- Evolutionary Conservation Biology
- Adaptive Speciation
- Evolution of Cooperation

An famous example – DD99

Dieckmann, U., and M. Doebeli (1999) **On the origin of species by sympatric speciation**. *Nature* 400:354-357.



Very simple conclusion :

$\sigma_c > \sigma_K$ ⇒ Evolutionary end-point where resource is maximal

$\sigma_c < \sigma_K$ ⇒ Branching

An famous example – DD99

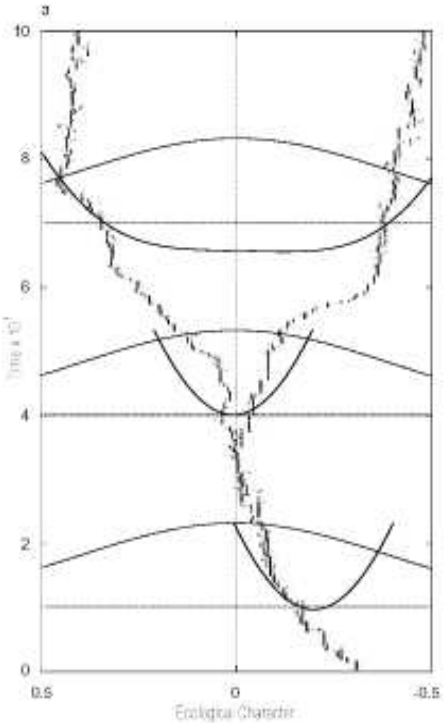


Figure 1: a) Evolutionary branching in the branching point $x_0 = 0$, the popula... show fitness functions (continuous curves) generated by the ecological interactions at different points in time (indicated by horizontal dotted lines). Selection changes from directional to disruptive when evolution reaches x_0. The resource distribution $K(x)$ has its maximum at x_0 and is shown for comparison (dashed curve). b) Same as a) but with multilocus genetics for the ecological character and random mating. Shading represents phenotype distributions (5 diploid and diallelic loci result in 11 possible phenotypes). Despite disruptive selection at the branching point (see insets), branching does not occur.

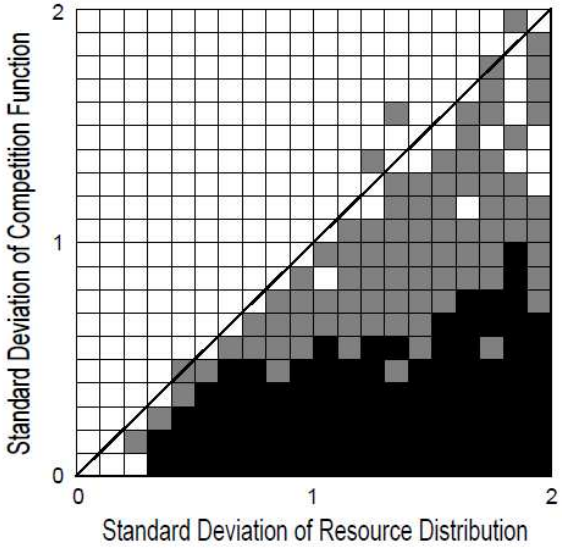


Figure 4: Combinations of standard deviations σ_K and σ_C of resource distribution $K(x)$ and competition function $C(x)$, respectively, that allow for evolutionary branching. Analytical results are available for the asexual model (see Methods) and predict branching for $\sigma_C < \sigma_K$, i.e. below the diagonal (black triangle). Conditions for branching in sexual populations (within 20,000 generations) are shown in gray when mating probabilities depend on the ecological character and in black when they depend on a marker trait.

An famous example – DD99

"Our results extend and contrast previous insights by showing that competition for unimodal resources can initiate sympatric speciation even if assortative mating depends on an ecologically neutral marker trait. […] Evidence is accumulating that ecology is important for speciation, and our theory may provide an integrative framework for understanding otherwise puzzling evidence for monophyletic origins of many sympatric species including cichlids, sticklebacks, snails, giant senecios, and anolis lizards. In all these cases it is likely that frequency-dependent mechanisms are important determinants of the species' ecologies."

Sic !

What's wrong with adaptive dynamics?

2005 JEB's target review is about adaptive dynamics

D. WAXMAN, S. GAVRILETS 20 Questions on Adaptive Dynamics

Gourbière & Mallet "Has adaptive dynamics contributed to the understanding of adaptive and sympatric speciation?"

Abrams "Waxman and Gavrilets' […] are probably correct in arguing that Adaptive Dynamics is insufficient to predict when sympatric speciation will occur"

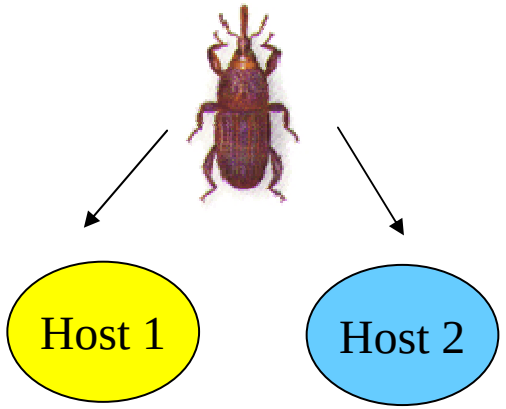
Barton & Polechova "adaptive dynamics is not plausible as an actual model of evolution under mutation and selection"

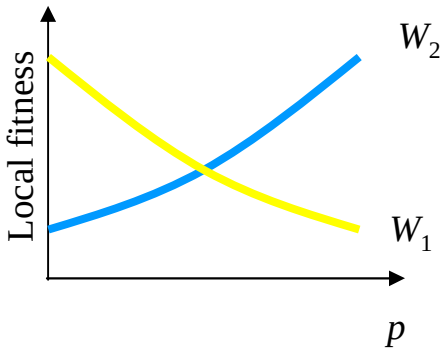
H. KOKKO Useful ways of being wrong
S. A. H. GERITZ, M. GYLLENBERG Seven answers from adaptive dynamics
J. A. J. METZ Eight personal rules for doing science
U. DIECKMANN, M. DOEBELI Pluralism in evolutionary theory

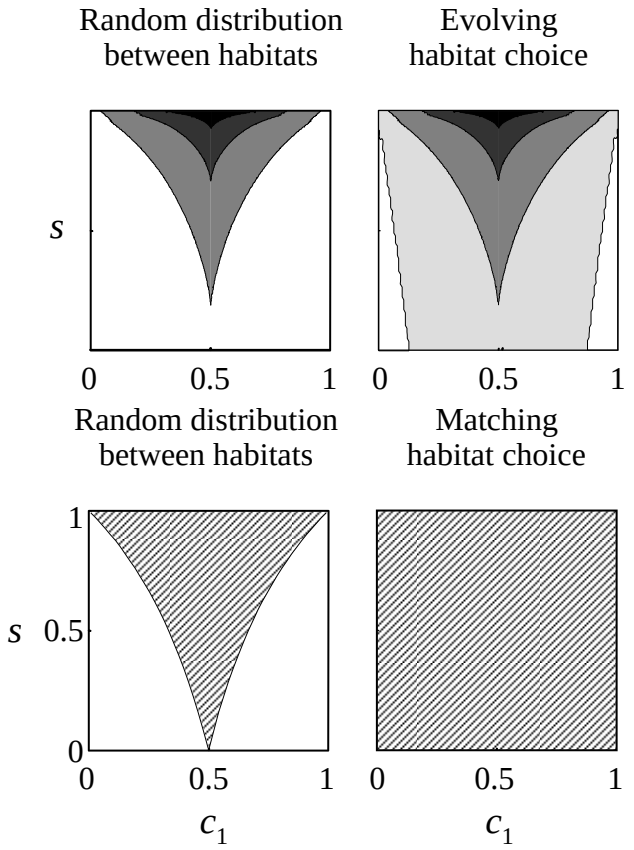
What's wrong with adaptive dynamics?

Although the basic assumptions of AD are well-established, their impact on the predictions still has to be evaluated

Example : small mutation effects







Ravigné et al. 2009

Any inverse trade-off strength γ — $\gamma = 0.2$ — $\gamma = 0.5$ — $\gamma = 0.9$ — $\gamma = 1.2$

Links between AD and empirical research

Barton & Polechova “Adaptive dynamics is a useful technique for understanding the qualitative behaviour of an evolving population”.

= Souce of inspiration rather than predictive models

Evolution, 58(2), 2004, pp. 245–260

EXPERIMENTAL EVIDENCE FOR SYMPATRIC ECOLOGICAL DIVERSIFICATION DUE TO FREQUENCY-DEPENDENT COMPETITION IN *ESCHERICHIA COLI*

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[3]*Department of Biology and Biochemistry, University of Houston, Houston, Texas 77204*

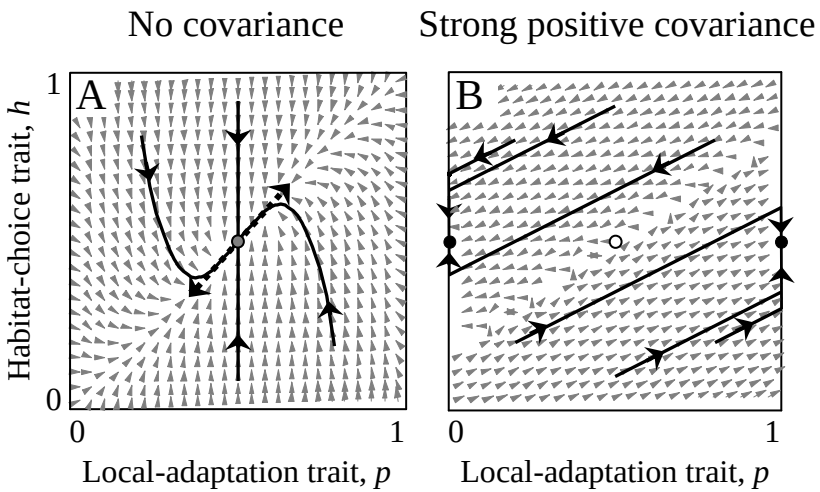
Abstract.—We investigate adaptive diversification in experimental *Escherichia coli* populations grown in serial batch cultures on a mixture of glucose and acetate. All 12 experimental lines were started from the same genetically uniform ancestral strain but became highly polymorphic for colony size after 1000 generations. Five populations were clearly dimorphic and thus serve as a model for an adaptive lineage split. We analyzed the ecological basis for this dimorphism by studying bacterial growth curves. All strains exhibit diauxie, that is, sequential growth on the two resources. Thus, they exhibit phenotypic plasticity, using mostly glucose when glucose is abundant, then switching to acetate when glucose concentration is low. However, the coexisting strains differ in their diauxie pattern, with one cluster in the dimorphic populations growing better in the glucose phase, and the other cluster having a much shorter lag when switching to the acetate phase. Using invasion experiments, we show that the dimorphism of these two ecological types is maintained by frequency-dependent selection. Using a mathematical model for the adaptive dynamics of diauxie behavior, we show that evolutionary branching in diauxie behavior is a plausible theoretical scenario. Our results support the hypothesis that, in our experiments, adaptive diversification from a genetically uniform ancestor occurred due to frequency-dependent ecological interactions. Our results have implications for understanding the evolution of cross-feeding polymorphism in microorganisms, as well as adaptive speciation due to frequency-dependent selection on phenotypic plasticity.

Key words.—Adaptive dynamics, diauxie, experimental evolution, phenotypic plasticity, sympatric speciation.

Evolution of Adaptive Dynamics

Already feasible…

- models with (very simple) sexual reproduction (Geritz & Kisdi 1999)
- non-equilibrium resident population dynamics
- accounting for traits population-level variances and covariances (Leimar 2009)
- plasticity



Ravigné et al. 2009

Conclusion

- Relatively simple techniques to gain insight into the complexities of frequency-dependent selection

- Particularly relevant to determine the qualitative shape of selection pressures (directional, stabilizing, disruptive or divergent) when the ecological context is key

  e.g., evolution of demographic parameters, joint evolution of traits, species coevolution (predator-prey, plant-herbivore, mutualisms, host-parasite)…

- Not adequate when genetic architecture really matters

  e.g., predicting the transient states of evolutionary dynamics evolution of reproductive isolation, sexual selection, kin selection…

Merci de votre attention